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## C:N:P ratios of freshwater benthic algae

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with 4 tables

**Abstract:** The measurement of internal C:N:P (carbon : nitrogen : phosphorus) ratios can be used as a tool to determine the nutrient status of freshwater benthic algae because it is both an easy and reliable method. It is possible to detect a severe nutrient limitation with the C:N:P method alone. A moderate limitation should be confirmed by other bioassays. This is shown by a review of published studies. C:N:P ratios of freshwater benthic algae at optimal (158:18:1 molar basis) and nutrient limiting conditions were derived from the literature. These values were used to state the nutrient status of freshwater benthic algae in Lake Erken, Sweden. The proposed values should be confirmed by more studies both in the laboratory and *in situ*, since there is still a lack of knowledge.

### Introduction

The importance of substrata as nutrient sources for freshwater benthic algae is still a field of challenging questions. I chose to compare the nutrient status of freshwater benthic algae growing on different substrates in Lake Erken, Sweden. Benthic algae tend to grow in a heterogeneous pattern (LOWE 1996). Therefore, it is necessary to process a great number of samples to characterize the scales of temporal and spatial heterogeneity that can be observed in these communities. Consequently, I needed a simple and reliable method for rapid assessment of the nutrient status of benthic algae.

Many methods are available to measure the nutrient status of algae (e.g. measurement of enzyme activities or nutrient uptake rates). The simplest method is the estimation of C:N:P (carbon : nitrogen : phosphorus) ratios. HECKY & KILHAM (1988) and HECKY et al. (1993) recommended the measurement of C:N:P ratios as a good method to estimate nutrient status of phytoplankton. BJÖRNSÄTER & WHEELER (1990) recommended the C:N:P method for marine benthic algae, and DUARTE (1990) recommended the method for marine seagrass. I will demonstrate in this paper that one can use the C:N:P method for freshwater benthic algae as well.

### C:N:P method

The principle of the C:N:P method is a comparison between the measured internal C:N:P ratio of the algae and an optimal ratio. This optimal ratio would occur in the algae when nutrients are not limiting nor in surplus.

Under P or N surplus algal P or N tissue level could be high, if the algae are able to store these nutrients. BJÖRNSÄTER & WHEELER (1990) showed that algae try to maintain a balanced internal N:P ratio. A surplus would not be optimal since the algae would waste energy on storage. Under P or N limitation, algal P or N tissue level would be low, because of the lack of sufficient ambient nutrients.

Therefore, under non-optimal (nutrient surplus or limitation) conditions algal C:N:P ratios would differ from the optimal ratio. For the effective use of the C:N:P method, the optimal ratio of the investigated algal population should be known. This optimal ratio is very difficult to obtain for several reasons. In practice, the "real optimal ratio" is replaced by an

empirically estimated ratio, derived from the literature. Literature values are rather "ratios occurring under obviously non-limiting conditions", but in the interest of simplicity I am going to call them "optimal ratios".

The first advantage of the C:N:P method is its simplicity. The determination of C and N is easy with automated CN analyzers. The determination of P by persulfate acid digestion is not complicated either. The researcher can store the samples after filtration. In this way it is possible to get a high number of replicates.

Second, the "nutrient history" of the algae is included, so not only the ambient nutrient situation is investigated, but also some time before sampling (BJÖRNSÄTER & WHEELER 1990, FONG et al. 1994). This gives a better picture of the real situation for the algal community.

Third, the nutrient situation can be studied without any manipulation. All of the physical, chemical and biological parameters are natural.

However, the C:N:P method has also disadvantages. Detritus and other non-algal material can influence the measured C:N:P ratios. Detritus, for example has more C in relation to N and P than algae (ALLAN 1995, MAKAREVICH et al. 1992). Bacteria on the other hand can play a role as a significant P-pool when their biomass is high (RHEE 1972, PETTERSSON et al. 1993). Separation is one possibility to solve these problems. Larger detritus and animals can be sorted out by hand. Filtration can separate algae from bacteria and small detritus. Some authors recommend filters with a pore size of 0.5–0.8  $\mu\text{m}$  (SAKSHAUG 1980, PORTER et al. 1988), others use filters with a pore size of 3  $\mu\text{m}$  (HARRIS 1986, ISTVÁNOVICS et al. 1990, PETTERSON et al. 1993). Also the use of a microscope as well as the calculations of the C:Chl *a* ratio can help to assess the amount of non-algal material in the sample. Furthermore, HECKY et al. (1993) considered in the case of phytoplankton, the impact of detritus on the C:N:P ratios of minor significance.

However, it is still a subject of controversy whether the C:N:P ratios can be altered by other factors than nutrients, for example by light or by grazing.

WYNNE & RHEE (1986) conclude that light can strongly influence the C:N:P ratios. The tissue content of C and N might be influenced more than the P content (WYNNE & RHEE 1986, NIELSEN 1992). Different algal species can obviously react in an opposite way: some species decrease their C and N content under increasing light (NIELSEN 1992), others increase it (MAGNUSSON et al. 1996). But even if the content is altered, the ratio remains often almost unchanged (GOLDMAN 1986, MAGNUSSON et al. 1996). Based on evidence provided in the literature, I concluded that the influence of light in a mixed natural community is of minor importance to the C:N:P ratios.

Grazing can also change the C:N:P ratios, but the pattern is as unclear as in the impact of light. Grazed communities might be higher in nutrients with lower C:N ratios (PETERSON et al. 1993, ROSEMOND 1993).

Another problem of the C:N:P method is the occurrence of different optimal ratios for different algal species (FAIRCHILD et al. 1985, BJÖRNSÄTER & WHEELER 1990, DUARTE 1990, HECKY et al. 1993, CHOPIN et al. 1996). An algal community could have a sufficient nutrient supply despite a high C:N:P ratio, only because the algal species of the community are adapted to low nutrient concentrations. But HECKY & KILHAM (1988) and HECKY et al. (1993), DUARTE (1990) and BJÖRNSÄTER & WHEELER (1990) showed that the interspecific variation of C:N:P ratios is smaller than the intraspecific variation. Therefore a difference of C:N:P ratios indicates rather a different nutrient situation than different algal species.

Despite all the mentioned doubts, the C:N:P method is still used successfully to estimate the nutrient status of marine and freshwater phytoplankton and marine benthic algae. The method is widely accepted (e.g. REDFIELD 1958, RHEE 1978, GOLDMAN et al. 1979, GORDON et al. 1981, ATKINSON & SMITH 1983, RAO & INDUSEKHAR 1987, FAGANELI et al. 1988, PAASCHE & ERGA 1988, HECKY & KILHAM 1988, HECKY et al. 1993, BJÖRNSÄTER &

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WHEELER 1990, PIHL et al. 1996). Optimally growing mixed natural phytoplanktic populations almost always have the Redfield ratio (C:N:P = 106:16:1 molar basis) as an optimal ratio (HECKY & KILHAM 1988, HECKY et al. 1993 and references therein). Therefore, the Redfield ratio is considered a community wide optimum nutrient ratio (BORCHARD 1996).

My intention is to judge, whether a researcher can use the C:N:P method for freshwater benthic algae as well. To my knowledge this is the first time that facts about the use of the C:N:P method for freshwater benthic algae are collected.

I searched for literature on C:N:P ratios of freshwater benthic algae. I looked especially for studies dealing with the change of algal C:N:P ratios after nutrient enrichment. A clear change of the C:N:P ratios after enrichment would support the reliability of the C:N:P method. I searched also for studies that connected the C:N:P method and other bioassays. If the outcome would be the same, this would further strengthen the validity of the C:N:P method. I tried to calculate median ratios for optimal nutrient status and limitation. I tried furthermore to identify distinct C:N:P ratios that would indicate limitation clearly. I searched for differences between algal taxa. I found that studies on nutrient status of freshwater benthic algae employing the C:N:P method are rather few. The studies are also very different: sometimes they give many values, sometimes only average results. I took medians from the reported values in the literature. When necessary, I converted the reported values to C:N:P ratios (molar basis).

## Results and discussion

### C:N:P ratios and enrichment studies

Table 1 shows the studies on freshwater benthic algae reporting C:N:P ratios with and without artificial or natural nutrient enrichment.

PETERSON et al. (1993) fertilized a whole tundra river with P. They reported an increase in C, N and P stocks of the diatom mat present and an increase of P relative to C and N. They also noticed a sharp increase in Chl *a* when they inhibited grazing.

ROSEMOND (1993) used small nutrient (P + N) releasing tiles in Walker Branch, a stream in Tennessee. She also recorded the influence of light and grazers. Algae (diatoms, green algae and bluegreen algae) growing on fertilized surfaces had on average lower C:P and N:P ratios. She noticed an increase in Chl *a* when light was increased and grazers were absent.

NEIL & JACKSON (1982) fertilized a shoreline site of Lake Erie with P. The present *Cladophora* reacted with decreased N:P ratios and a rapid growth.

ROSEMARIN (1982) used short term batch cultures of *Cladophora* to show the effect of P + N enrichment on tissue nutrient level. N:P ratios decreased after addition of P + N. Growth was not determined.

Table 1. Change of C:N:P ratios (molar basis) and biomass of freshwater benthic algae after an increase in ambient nutrients (P and/or N).

algal community	increased nutrient	kind of enrichment	C:N	C:P	N:P	change in biomass	source
diatoms <i>in situ</i>	P	artificial	10→9	207→121	22→13	increased	PETERSEN et al. 1993
diatoms <i>in situ</i>	P+N	artificial	20→23	443→301	22→13	no change	ROSEMOND 1993
green/bluegreen algae <i>in situ</i>	P+N	artificial	12→12	603→465	49→40	increased	ROSEMOND 1993
<i>Cladophora in situ</i>	P	artificial	*	*	72→58	increased	NEIL & JACKSON 1982
<i>Cladophora in vitro</i>	P	artificial	*	*	19→8	*	ROSEMARIN 1982
<i>Cladophora in situ</i>	N	natural	34→11	382→220	12→20	*	LOHMAN & PRISCU 1992
<i>Cladophora in situ</i>	P(+N)	natural	*	*	42→17	no change	FREEMAN 1986
epiphyton <i>in situ</i>	P	natural	9→9	439→158	51→18	decreased	SARVALA et al. 1982

If necessary, original values were converted into median C:N:P (molar basis) values. \* not reported.

LOHMAN & PRISCU (1992) monitored the *Cladophora* population of Clark Fork of the Columbia River, Montana, influenced by wastewater. They recorded decreased C:N and C:P ratios and increased N:P ratios after a N peak in the water. They did not determine growth.

FREEMAN (1986) studied *Cladophora* in the Manawatu River, New Zealand and observed ambient nutrient concentrations together with C:N:P ratios and biomass. He showed a decrease in N:P ratios after a P peak in the ambient water, but biomass was primarily controlled by river flow. FREEMAN (1986) did not see a distinct correlation of low N:P ratios and high biomass.

SARVALA et al. (1982) monitored the epiphyton of an oligotrophic lake in Southern Finland. A low ambient P concentration in spring and early summer was followed by high N:P ratios. An increase of P later in the year led to lower N:P ratios but not to higher growth, most likely because of the low temperatures in autumn.

All of the presented studies show that the predicted change in C:N:P ratios is due to nutrient enrichment. The studies with an artificial nutrient enrichment also showed an increase in algal biomass after enrichment.

#### C:N:P ratios and other bioassays

Some studies use both C:N:P ratios and other tests to estimate the nutrient status of freshwater benthic algae.

In their studies on *Cladophora* of the Great Lakes, AUER & CANALE (1980, 1982) and CANALE et al. (1982) stated that P uptake is closely coupled both to external P as well as internal P. They developed a model showing that the P uptake depends on the external P concentration until the internal stores are filled and a feedback mechanism inhibits further P uptake. The model calculated a high P uptake at low internal P levels. ROSEMARIN (1982) showed a similar pattern for N uptake.

FREEMAN (1986) found a close coupling of P and N tissue levels and other tests like P and N nutrient uptake, estimation of luxury P and APA (alkaline phosphatase activity). He suggested seasonal P limitation in his study and based his suggestion on high N:P ratios, a high P uptake, a high APA and low luxury P.

ROSEMOND (1993) found a decreased APA together with decreased C:P and N:P ratios under nutrient (P + N) enrichment. LOHMAN & PRISCU (1992) reported a low N uptake during a high ambient N concentration and at the same time a decrease of the C:N and an increase of the N:P ratios.

REUTER et al. (1986) investigated an N-deficient lake, Lake Tahoe in California-Nevada. They recorded a relatively high C:N ratio in the bluegreen algae present. Later in the season they measured decreased C:N ratios along with a high nitratoreductase activity (high use of nitrate). The authors had expected a high nitratoreductase activity under N limitation and had no explanation for their results. However, I consider the measurement of nitratoreductase activity not to be a useful method to estimate N limitation. It is rather a measurement of nitrate usage. Nitratoreductase activity can indeed indicate a shortage of ammonium, but does not necessarily indicate a N limitation. The algae in the study of REUTER et al. (1986) filled their N stores with nitrate instead of ammonium. The decreased C:N ratios indicated correctly that N limitation no longer persisted.

Four of the presented studies that investigated nutrient limitation reported a distinct correlation between the C:N:P method and other bioassays. One study failed to show this correlation. However, in that case the chosen bioassay was not useful to show a N limitation.

#### C:N:P ratios of freshwater benthic algae

Table 2 shows the C:N:P ratios of freshwater benthic algae measured *in situ*. I included the nutrient conditions for the investigated algal community, if the researcher made a comment on it.

The reported values for C:N:P ratios of freshwater benthic algae have a broad range. However, regardless of the nutrient situation, most of the values reported for marine benthic algae are higher (ATKINSON & SMITH 1983). Most values of freshwater benthic algae are reports on diatoms and *Cladophora* communities. The reported values for diatoms are in general lower than those for *Cladophora*, indicating a lower structural carbon and/or a higher nutrient content for diatoms. The ratios I measured in Lake Erken represent no exception.

The values of Table 3 and 4 are derived from Table 2. I could not use all values to calculate medians, because some researchers did not report the nutrient situation. Moreover, most of the researchers estimated the nutrient situation only roughly. Furthermore, even if in some cases I could calculate medians from several values, I had to rely on a few average values in other cases. Therefore the tables present only a gross overview of the field.

Table 3 shows the C:N:P ratios at nutrient limitation and at non-limiting conditions.

At non-limiting conditions the algae should have their optimal C:N:P ratio. The optimal median value is 158:18:1, which is close to the Redfield ratio. However, the estimation of the theoretical optimal C:N:P ratio suffers from a proper estimation of the nutrient conditions. Moreover, the investigated studies made no distinction between optimal and surplus conditions. C:N:P ratios would be lower than the theoretical optimal ratio under surplus conditions. The estimated optimal C:N:P ratio would then be too low, if studies with surplus conditions are included in the calculation.

Under P limitation the C:P value is slightly higher and the N:P value is clearly higher than the optimal value. The C:N ratio is the same as for optimal conditions. The relatively low C:P value is likely a result of the paucity of the values.

The median C:N ratio under N limitation is clearly higher than the optimal value, and there is no overlap with the optimal or P limited values. The N:P value is clearly lower than the optimal value. The C:P ratio is not only higher than the optimal value but it is even higher than under P limitation. A P and N limitation is shown by overall increased C:N:P ratios. The values lie between those for distinct P or N limitation. The C:P values under P and N limitation are even higher than under P or N limitation alone.

Table 4 shows ratios that indicate a nutrient limitation clearly. The C:P value for P limitation is somewhat weak as stated above. It is prudent to consider all three ratios C:N, C:P and N:P to estimate the nutrient situation. But it is also apparent that the calculated values for freshwater benthic algae fit very well to literature reports: ALLAN (1995) indicated N limitation with  $N:P < 10$  and P limitation with  $N:P > 30$  in freshwater benthic algae. The N:P value is the same for benthic marine algae (BJÖRNSÅTER & WHEELER 1990, CHOPIN et al. 1996). Phytoplankton values are lower (HECKY et al. 1993 and references therein) indicating that marine and freshwater benthic algae could have a different metabolism than phytoplankton. This is valid for both marine and freshwater algae. An explanation could be the possibly higher structural carbon of benthic algae (ATKINSON & SMITH 1983).

#### Nutrient situation of benthic algae and phytoplankton in Lake Erken

I assessed the nutrient status of the epilithon and epiphyton of Lake Erken, Sweden by relating the ratios found in 1996 to Table 4. The epilithon were slightly N and P limited throughout the year, the P limitation was somewhat higher in summer. The epiphyton were N limited only in autumn, if at all. The values showed instead a severe P limitation in summer.

It is now possible to compare the nutrient situation of the benthic algae with the nutrient situation of the phytoplankton of Lake Erken, investigated in previous studies (ULÉN 1971, PETTERSSON 1980, ISTVÁNOVICS et al. 1992, PETTERSSON, et al. 1993). In general, the phytoplankton of Lake Erken are severely P limited in spring/summer and can be N limited in late summer/autumn. The pattern is therefore the same as in the epiphyton. The onset of the P limi-

Table 2. C:N:P ratios (molar basis) of freshwater benthic algae estimated *in situ* and their nutrient status as stated by the authors.

algal community	nutrient status	C:N	C:P	N:P	locality of investigation	source
diatoms	not limited	8-9	99-142	11-15	Kuparuk River, Alaska	PETERSEN et al. 1993
	P limited	9-11	168-246	13-31	Kuparuk River, Alaska	PETERSEN et al. 1993
	P & N limited	20	443	22	small tributary of Walker Branch, Tennessee	ROSEMOND 1993
	*	23	301	13	small tributary of Walker Branch, Tennessee	ROSEMOND 1993
	*	11	89	8	Lake Naroch, Belorussia	MAKAREVICH et al. 1992
	*	6	*	*	Lake Tahoe, California-Nevada	LOEB 1981
	*	4	*	*	shallow pond, Michigan	HUNTER 1980
	not limited	10-11	231-369	23-32	Lake Erie, Ohio	LORENZ & HERDENDORF 1982
	not limited	*	*	16-18	Manwatu River, New Zealand	FREEMAN 1986
	P limited	*	*	33-50	Manwatu River, New Zealand	FREEMAN 1986
<i>Cladophora spec.</i>	P limited	*	*	47	Lake Ontario, Canada	ROSEMARIN 1982
	P limited	*	*	72	Lake Erie, Canada	NEIL & JACKSON 1982
	N surplus	11	220	20	Columbia River, Montana	LOHMAN & PRISCU 1992
	N limited	30-51	358-485	10-12	Columbia River, Montana	LOHMAN & PRISCU 1992
	P & N limited	*	*	29-44	Manwatu River, New Zealand	FREEMAN 1986
	*	10	208	20	Lake Erken, Sweden	ULÉN 1971
	*	9	*	*	shallow pond, Michigan	HUNTER 1980
	N limited	16	192	12	streams on Signy Island, Antarctica	HAWES 1989
	P & N limited	12	603	49	small tributary of Walker Branch, Tennessee	ROSEMOND 1993
	*	12	465	40	small tributary of Walker, Branch, Tennessee	ROSEMOND 1993
greenalgae						
green- and bluegreen algae						
bluegreen algae						
diatoms, green- and bluegreen algae						

green- and bluegreen algae	N limited P & N limited	16 12	192 603	12 49	small tributary of Walker Branch, Tennessee	HUNTER 1980 HAWES 1989 ROSEMOND 1993
	*	12	465	40	small tributary of Walker, Branch, Tennessee	ROSEMOND 1993
bluegreen algae	N limited	14	*	*	Lake Tahoe, California-Nevada	REUTER et al. 1986
	*	14	*	*	Lake Tahoe, California-Nevada	LOEB 1981
diatoms, green- and bluegreen algae	*	12-17	31-176	3-12	Lake Naroch, Belorussia	MAKAREVICH et al. 1992

Table 2. Continued.

algal community	nutrient status	C : N	C : P	N : P	locality of investigation	source
<i>Nitella</i>	*	26	312	12	lake (not specified)	MARTINOVA 1993
epiphyton	not limited	9	158	18	Lake Pääjärvi, Finland	SARVALA et al. 1982
	P limited	9	439	51	Lake Pääjärvi, Finland	SARVALA et al. 1982
epiphyton	?				Lake Erken, Sweden	KAHLERT, unpubl. data
spring		10	194	20		
summer		8	264	38		
autumn		12	196	19		
epilithon	?				Lake Erken, Sweden	KAHLERT, unpubl. data
spring		12	249	20		
summer		12	266	25		
autumn		12	275	22		

If necessary, original values were converted into median C : N : P (molar basis) values. \* not reported.

Table 3. C : N : P ratios (molar basis) of freshwater benthic algae indicating optimal, P and/or N limited conditions. Median values and range derived from Table 2.

nutrient status	C : N	C : P	N : P
optimal	9 (8-11)	158 (99-369)	18 (11-32)
P limited	9 (9-11)	246 (168-439)	47 (13-72)
N limited	23 (14-51)	358 (192-485)	12 (10-12)
P & N limited	16 (12-20)	523 (443-603)	37 (22-49)

Table 4. C : N : P ratios (molar basis) indicating nutrient limitation.

nutrient status		freshwater benthic algae	marine benthic algae	freshwater phytoplankton	marine phytoplankton
P limited	C : P	>369		>129	>150
	N : P	> 32	>31	> 22	> 20
N limited	C : N	> 11		> 8	
	N : P	< 12	<12		< 10
P & N limited	C : N : P	all values relatively high			

source: freshwater benthic algae: Table 2; marine benthic algae: BJÖRNSÅTER & WHEELER 1990, CHOPIN et al. 1996; phytoplankton: HECKY et al. 1993 and references therein.

tation seems to be somewhat earlier in the phytoplankton than in the epiphyton. The epilithon on the other hand have a completely different nutrient status. The P limitation in summer is not severe and the N limitation occurs throughout the whole year.

### Conclusions

Enrichment studies and studies connecting the C:N:P method with other bioassays showed that the measurement of C:N:P ratios is a reliable method to estimate the nutrient status of freshwater benthic algae. Some of the reported values did not fit, but the general pattern was clear.

The optimal ratio for freshwater benthic algae is 158:18:1 with a relatively large variation.

It is possible to estimate severe P limitation with N:P ratios and N-limitation with C:N and N:P ratios (see Table 4). Very high C:N:P ratios were always associated with nutrient limitation.

If the algae are only slightly limited it is not so easy to detect this limitation. The researcher has to consider the whole situation, including the ambient nutrient level, the amount of detritus, bacteria, grazing, light and the existing algal taxa. One must consider all three C:N:P values (C:N, C:P, N:P) and should combine the C:N:P method with other bioassays.

The present overview can only be preliminary, because the reported values are too few and there are no laboratory studies on C:N:P ratios of freshwater benthic algae. Additional attention should be given to the relationship of growth rate to C:N:P ratios. Although the calculation of the medians suffers from proper estimations of the nutrient situation and from a distinction between optimal and surplus conditions; the estimated values fitted well with those reported from the literature.

We need more information about optimal C:N:P ratios. It is most reliable to derive them from laboratory studies, therefore we have to improve the culture of freshwater benthic algae. More studies both in laboratory and *in situ* are necessary to address the lack of knowledge on the nutrient status of freshwater benthic algae.

In general I consider the measurement of C:N:P ratios as a useful method to scan the nutrient status of freshwater benthic algae since it is an easy and reliable method.

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## Induction of bacterioplankton

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**Abstract:** Measurements of bacterial phosphatase,  $\beta$ -glucosidase and leucine aminopeptidase in eutrophic Lake Erken in Sweden during summer 1999. Bacterioplankton had low abundance and biomass. A chlorophyll maximum occurred in the water column. Phosphorus through the synthesis of bacterial phosphatase caused the synthesis of alkaline phosphatase, leucine aminopeptidase, and productivity of bacterioplankton was high.

The dominant part of organic matter in the water column consists of simple molecules that can be directly utilized by bacteria (GELLER 1985). The polymeric transformations through enzymatic action of water ecosystems can be explained by extracellular enzyme processes.

Exoenzymes (CHROST 1999) outside the cytoplasmic membrane are catabolic enzymes (CHROST 1999). This synthesis is under a catalytic control by the end product. Further signal of substrate availability is given by the end product.

Alkaline phosphatases,  $\beta$ -glucosidases, and leucine aminopeptidases (sensu stricto phosphatases) are widely distributed in the water column and are associated with both algal and zooplankton (of  $\beta$ -linked disaccharides) and leucine aminopeptidase associated with heterotrophic bacteria.

The purpose of this work was to study the progression of a summer development (biomass production) to their end product, the potential food source for pelagic bacteria.